VARIABLE NECTAR REWARDS FOR HUMMINGBIRDS IN *BOMAREA* SP. (AMARYLLIDACEAE)

CHERYL B. SHANNON, EMILY M. MAHAR, MARC N. CONTE, AND KATHERINE W. MANARAS

Abstract: *Bomerea* sp., which depends on hummingbird pollinators, faces the challenge of maximizing outcrossing while minimizing energy investment in flower and nectar. We hypothesized that *Bomarea* sp. produces a small number of high nectar reward flowers on each plant (bonanza strategy) to manipulate pollinator behavior, and that hummingbirds will visit a greater proportion of flowers on plants that offer a higher average energy reward. As predicted, there was a non-normal distribution of nectar across flowers, and hummingbirds tended to visit a greater proportion of flowers on plants with increased rewards. We suggest three possibilities for why *Bomarea* sp. do not more nectar in nature: 1) costs of increased nectar production outweigh the benefits of increased flower visitation, 2) increasing the amount of nectar acquired per plant decreases the total number of plants that each pollinator will visit, and 3) increasing the number of flowers visited per plant increases the probability of self-fertilization. Apparently, *Bomarea* sp. has evolved a variable pattern of nectar distribution across flowers to manipulate hummingbird in a way that flowers which is optimal for plants.

Key Words: coevolution, hummingbird pollination, nectar manipulation, optimal foraging

INTRODUCTION

Many tropical plants face the challenge of sexual reproduction in an environment where conspecifics are rare. Many species require outcrossing for reproduction and rely on biotic pollinators for outcrossing (Hartshorn 1983). These plants face the challenge of providing nectar rewards in a way that simultaneously attracts visitors, maximizes the probability that visitors will also visit other plants, and minimizes the costs of producing flower and nectar rewards. One possible strategy employs high variance in nectar volume distribution across flowers to encourage the pollinator to visit multiple flowers in search of the few individual flowers on the plant with high energy rewards (Feinsinger 1978).

Bomarea sp, (Amaryllidaceae) presents a single inflorescence of red tubular flowers and depends on hummingbirds for pollination (Skutch and Stiles 1989). We hypothesized that *Bomarea* distributes nectar among flowers such that the frequency distribution of nectar volume among flowers is skewed toward low nectar volume, thereby encouraging pollinators to visit multiple flowers, while searching for the few flowers with high nectar rewards. Based on optimal foraging theory (Begon et al. 1990), we further predicted that hummingbird pollinators will visit a greater proportion of flowers on plants with more nectar per flower.

METHODS

This study was conducted 28 - 29 January 2000 at the Cuerici Biological Station, Costa Rica. To test our hypothesis regarding the distribution of nectar volume within inflorescences, we haphazardly chose three *Bomarea* plants growing along the road leading to the station. These inflorescences were covered with cheese cloth for 24 hours to prevent nectar removal, and permit the accurate measure of total daily nectar production per flower. On 29 January, we used capillary tubes to measure the volume of nectar within each flower. On each inflorescence, we analyzed the frequency distribution of nectar volumes among flowers using a Shapiro-Wilk test for normality. We also compared mean nectar volume per inflorescence between plants (using a Welch ANOVA to account for the differences in variances across plants). Finally, we compared the variance in nectar volumes among plants using a Brown-Forsythe test.

Bird pollination was observed between 06:00 and 14:00, 29 January, in the meadow 1 km S of the Ceurici Biological Station. The evening before observations, we haphazardly selected 10 *Bomarea* plants in this location and added 20 µl of 15% sugar solution into every flower on the inflorescences of five of the plants. The other five plants were left as controls. All inflorescences were then covered overnight to prevent nectar depletion prior to our observations. We uncovered each inflorescence 5 min before the first observation on each plant. We observed all plants during monitoring periods that lasted 1.5 to 2.5 h and quantified the mean proportion of flowers visited per pollinator visit to each plant. Control and experimental plants were compared using a Student's t-test.

RESULTS

The distribution of nectar volume within flowers of the same plant was non-normal for all three sample plants (Fig. 1; W = 0.83, 0.82, and 0.77 for plants 1 to 3, respectively; $p < 0.001$ for each). Each distribution was skewed to the right (Fig. 1), with the majority of flowers in an inflorescence having little or no nectar and a few having high nectar volumes. There were differences among plants in mean nectar volume per flower ($F_{2,80} = 5.72$, $p = 0.007$), and significant differences among plants in the variance among flowers ($F_{2,80} = 3.62$, $p = 0.03$). We observed multiple species of hummingbirds visiting *Bomarea* plants, including the purple-throated mountain gem (*Lampornii caldaena*) and the magnificent hummingbird (*Eugenes fulgens*). Birds visited a larger proportion of flowers on plants with added nectar than on controls, although the trend was only marginally significant (Fig. 2; $t = 2.04$, $df = 9$, $p = 0.07$).

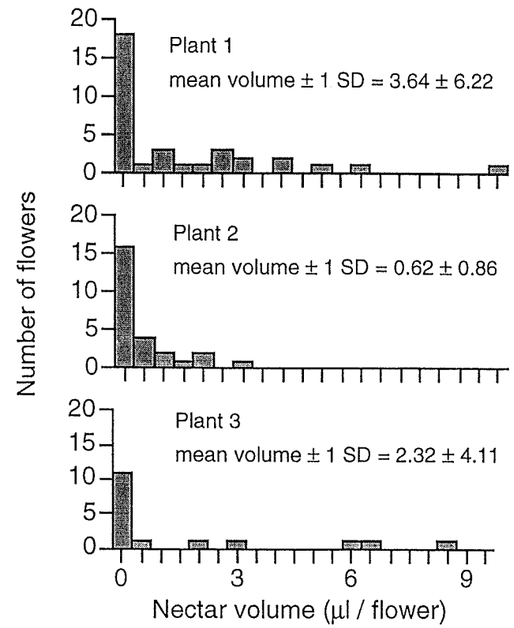

Figure 1. Frequency distributions of nectar volume among flowers of three Bomerea inflorescences.

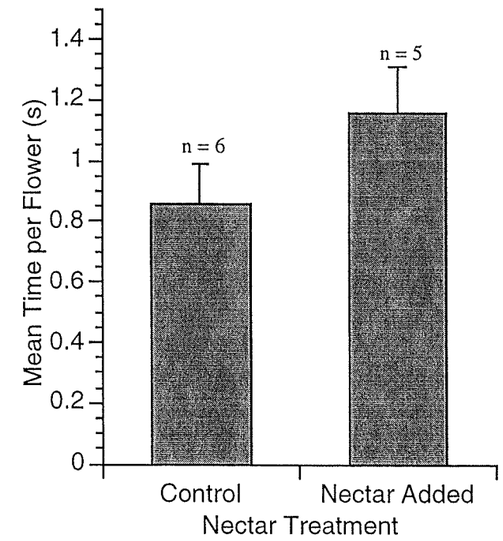

Figure 2. Time a hummingbird spends at each flower on a plant during a single foraging visit ($t = 1.497$, $df = 9$, $p = 0.1687$). Means + 1 SE.

Discussion

Bomarea sp. distributes nectar unevenly among flowers within inflorescences, indicating that they are employing the strategy of offering occasional bonanza rewards to pollinators. If the average nectar rewards are increased, without altering the variance, hummingbirds visit more flowers per plant, which the question of why *Bomarea* sp. does not provide larger average rewards to visitors. We suggest three possible explanations. First, plants may be unable to increase nectar production because they lack the carbohydrate resources. Second, it may not be in the best interest of the plant to maximize flower visitation on a plant. Increasing nectar volume could decrease the total number of plants visited by each hummingbird, thereby decreasing the genetic diversity of the pollen load on each bird. If the bird received more calories at each plant, then its caloric needs could be met by visiting fewer plants. Third, as the number of flowers visited per plant increases, the probability of self-pollination must increase. Maximum outcrossing probably requires some balance between the number of flowers visited per plant with the number of plants visited.

Bomarea sp. has evolved a variable pattern of nectar distribution across flowers in apparent response to the foraging behavior of hummingbirds. This relationship is based on simultaneously satisfying the food needs of the hummingbirds and the pollination needs of *Bomarea* sp. The coevolution of *Bomarea* and its hummingbird pollinators points to the importance of genetic outcrossing to plant individuals.

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